



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE SACRUM OF THE LACERTILIA.

ROY L. MOODIE,

THE UNIVERSITY OF CHICAGO.

The question of the morphology of the transverse processes of the sacral vertebræ of the *Lacertilia* seems never to have been definitely settled. There are extremely diverse statements in our various works on zoölogy concerning the exact nature of these processes. So far as I have been able to determine no one has ever taken up the study of the young stages of the lizards in order to determine this point. At the suggestion of Dr. S. W. Williston I have undertaken such a study while engaged in clearing the young and adult stages of a number of reptiles in the course of an extensive investigation on the epiphyses of the Reptilia.

The problem as it presents itself is whether or not the *Lacertilia* possess sacral ribs. If they do, there should be separate centers of ossification for these elements and we may confidently expect to find them in the embryonic condition. If there are no ribs, there should be no separate centers of ossification nor would sutures of separation of the ribs from the centra persist in the young of the lizards. The question as to whether the lizards ever had sacral ribs is not fully discussed. If the forerunners of the lizards had such ribs there would probably be a cartilaginous remnant of them in the embryo.

The material investigated includes the young and adult stages of representatives of five families of the *Lacertilia*, viz.: (1) Chameleoniidæ — *Chameleon owenii* Grey, two specimens, one young and one adult from Batanga, German East Africa. (2) Iguanidæ — *Iguana* sp. ?, one young specimen from Mexico. *Phrynosoma douglassi hernandesi* Girard, three specimens, two young and one adult, taken in Natrona Co., Wyoming, this past summer by the writer. *Sceloporus* sp. ?, one young specimen from Mexico. *Sceloporus chrysostictus* Cope, nine specimens, eight young and one adult from Zopopan near Jalisco, Mexico on the semi-arid upland

plains collected by W. L. Tower. (3) Teiidae — *Cnemidophorus sexlineatus* Linné, ten specimens, one adult and nine embryos from Mexico. (4) Agamidae — *Draco volans* Linné, one adult specimen from the East Indies. (5) Helodermatidae — *Heloderma suspectum* Cope, one adult specimen.

The specimens were cleared by the Schultze (1) method recently recommended by Dr. Mall (2) and more fully set forth by Hill (3). The method was adopted at the suggestion of Dr. Lillie and experiments have been made on clearing the young and adult stages of all groups of the Vertebrata except the fishes. The methods used are essentially those followed by Dr. Mall and need not be enumerated here. For a complete statement of the method the reader is referred especially to Hill's paper where Dr. Mall's methods are fully outlined. The Schultze method is an excellent one for demonstrating the intimate relations of the bones and cartilages of small animals and deserves to come into more general use as a method for laboratory demonstration.

Among the many recent writers on the lizards Friedrich Siebenrock seems to be the only one who has a definite conception of the true nature of the transverse processes of the sacral vertebræ of the *Lacertilia*. Cope with all of his keen insight and his wide acquaintance with fossil and recent reptiles seems not to have comprehended the unique character of the lacertilian sacrum. This seems the more remarkable since Cope did more on the lizards than any other naturalist. Cope's observations, however, are in some respects hasty and much of his work will need thorough revision. As an example of this he states on page 163 of his large work on the reptiles of North America, in speaking of the crocodiles: "There are two sacral vertebræ and no sacral ribs." But in the sacrum of the crocodiles there are no transverse processes and there *are sacral ribs*.

Siebenrock in writing on the skeleton of *Lacerta simonyi* Steind. (4) makes the following statement concerning the transverse processes of the lacertilian sacral vertebræ: "Die Frage über die morphologische Bedeutung der Querfortsätze an den Sacralwirbeln der Saurier sieht noch einer entscheidenden Lösung entgegen. Nach Gegenbaur (5) könnte man sie sowohl mit den praesacralen Rippen als auch mit den postsacralen Querfortsätze vergleichen,

so dass die Homologie zwischen Rippen und Querfortsätze ergeben wurde. Hoffman (6) glaubt jedoch annehmen zu dürfen, dass dieselben selbständig ossificiren und daher den Rippen entsprechen, obwohl der von Hoffman untersuchte *Monitor*-Embryo in der Entwicklung schon zuweit vorgeschritten war, um die Trennung der Querfortsätze vom Wirbeln constatiren zu können. Diese Trennung kann sich aber sogar an ausgewachsenen Thieren erhalten, wie von mir in drei Fallen und zwar an einem Skelete von *Hoplurus*, *Tropidurus*, und *Uromastix* wahrgenommen wurde. Denn der erste Sacralwirbel besitzt Rippen anstatt der Querfortsätze, welche dem Wirbel nicht allein durch eine Naht wie bei den Krokodilen und Schildkröten getrennt werden, sondern mit demselben sogar gelenkig verbunden sind."

In his contribution to the subject of vertebral assimilation Siebenrock (7) describes several cases such as he mentions in the above quotation and figures the condition in the sacra of *Uromastix spinipes* Merr. and *Lacerta simonyi* Steind. where the first sacral vertebra as Siebenrock calls it but which is in reality a posterior dorsal, bears a rib. Cope (8) likewise, mentions such a case as occurring in the vertebral column of *Phrynosoma* and Siebenrock has found the same condition in that genus. Such a condition, however, cannot be interpreted to mean three sacral vertebrae as Siebenrock believes. The vertebra assimilated is not a morphological sacral but merely a functional one and on that account cannot be called a true sacral. Such a condition as Siebenrock describes is of frequent occurrence among the other reptiles. The appearance of a rib in this situation is not a very remarkable occurrence since there are ribs in this situation in the primitive vertebrates and the occurrence of this rib in the lizards may confidently be regarded as a persistence of the embryonic condition in which the sacral ribs remain as vestiges. In the sacrum of *Lyriocephalus* Siebenrock (12) describes a vestige which may be interpreted to be a remnant of the sacral rib.

A close study of my material clearly shows that there are no sacral ribs in the modern lizards. The ilia are always attached directly to the *transverse processes* of the two sacral vertebrae. In the young specimen of *Chameleon owenii* Grey the transverse processes of the two sacral vertebrae are of equal size and are

very short. They arise broadly from the centra of the vertebræ. The same may be said of the adult specimen. In the *Phrynosoma* specimens a nearer approach to the ancestral condition of the vertebrate sacrum is seen. Gegenbaur (13) is of the opinion that the sacrum of the vertebrates was primitively of but one vertebra

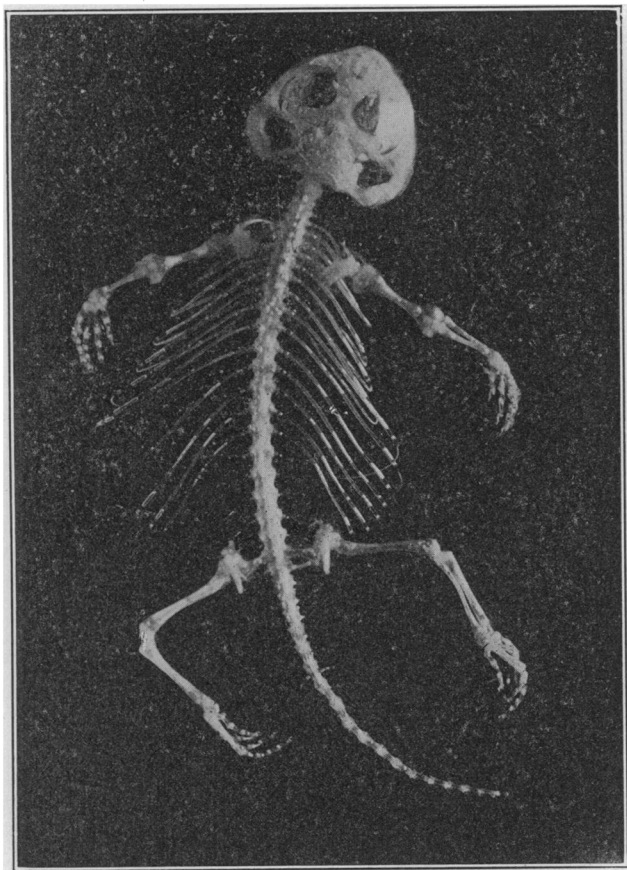


FIG. 1. Skeleton of *Phrynosoma douglassi hernandesi*. Girard.

as is found in the modern amphibians. Such a condition is what would be expected. In *Phrynosoma* the first sacral vertebra bears large stout transverse processes with expanded ends. The second sacral bears much smaller processes but they are still larger than the processes on the succeeding pygals. These like-

wise arise from broad bases. The disparity in size between the two pairs of processes of the sacrals is such that the anterior pair appears to bear all of the burden of support (Fig. 1). In the specimen of *Sceloporus* the transverse processes are of more nearly equal size but are longer than in the *Chameleon*. In *Draco* the processes are stout and end broadly. In *Iguana* the transverse processes of the sacrals are of equal strength and have broad ends. In *Heloderma* there are broad transverse processes supporting the pelvis. In *Cnemidophorus* the sacral vertebræ bear stout transverse processes of which the anterior pair is the larger.

One would expect to find a suture of separation between the processes and the sacral centra of young lizards did such a separation really exist but even in the youngest of my specimens, *Sceloporus*, which are two days old and in which the epiphyses are just beginning to appear as minute centers of ossification, there is not the slightest indication of any separation between the sacral centra and their transverse processes. But we have more positive evidence still, that there are no sacral ribs in the lizards. In an embryo of *Cnemidophorus sexlineatus* Linné which measures 24 mm. from the tip of the snout to the base of the tail and in which the diaphyses of the limb bones are only one half ossified and the epiphyses have not appeared at all, the broad connection of the transverse processes to the centra of the vertebræ is clearly apparent. Furthermore the ossification of the processes is seen to be proceeding outward from the body of the vertebra into the transverse process so that there is no chance for a separate center of ossification in the processes. It can thus be very definitely stated that the Lacertilia occupy an isolated place among all other known reptiles in *not having any sacral ribs whatever*.

In nearly all of our modern text-books on zoölogy the statement is made that there are sacral ribs in the lizards and in none is a statement made to the contrary. Even Huxley (9) in his work on the anatomy of vertebrated animals states that there are sacral ribs but does not discuss the matter. Parker and Haswell (10) in their "Text-Book of Zoölogy" make the statement: "The sacral vertebræ have short and strong expanded processes — *the transverse processes* — which abut against the ilia,

these are separately ossified and are to be looked upon as sacral ribs." Gadow (11) in his work on "Amphibia and Reptiles" says: "The pelvis is attached to two vertebræ by means of several ribs." I have given in the bibliography, under (10), a complete list of our general works on zoölogy in which there is any statment made concerning the sacral ribs of the Lacertilia. They all agree pretty well that there are sacral ribs.

In order to be sure that there are sacral ribs among our living reptiles other than the lizards I have investigated both the young and adult stages of the turtles, crocodiles and *Sphenodon*. In a young turtle, *Chelydra*, 44 mm. in length, the separation between the vertebral centra and their sacral ribs is clearly apparent. In a young alligator, six inches in length, the sutures between the sacral ribs and the centra are clearly seen as they are also in a specimen something over four feet in length. The sutures persist in the adult of the alligator and are found in the young and adult of the *Gavialis gangeticus* Gmel., thus completely disproving Cope's statement that there are no sacral ribs in the crocodiles. In *Sphenodon* the sacral ribs are distinct. We know that among the Dinosauria the sacral ribs did not fuse with the centra until late in life. There is in the Field Museum a specimen of a young *Morosaurus*, as identified by Mr. Riggs, which is of considerable size, and yet the sacral ribs are clearly separated from the centra. Marsh has figured a similar condition in the sacrum of *Morosaurus lentus* on Plate XXXIII. of his "Dinosaurs of North America." Hatcher in his paper on *Haplocanthosaurus* (14) gives a lengthy and very interesting discussion of the sacral ribs in the Dinosauria. He expresses it as his opinion "*that there are no true sacral ribs homologous with these elements in the tailed amphibia and that the so-called ribs are really homologous with the parapophyses or inferior branches of the transverse processes.*"

But Mr. Hatcher is mistaken in his conception of the homology of these elements above mentioned. If it is true, as he states it is, that the sacral ribs (parapophyses, Hatcher) and the transverse processes of the caudal vertebræ arise from distinct ossificatory centers in the sauropod dinosaurs then we have in these animals a primitive condition and especially as regards the

caudal ribs, recalling, as it does, the condition which exists in the modern tailed amphibians (*Menopoma*, *Necturus*). McGregor (15) has described separate caudal ribs in the Phytosauria and also describes free sacral ribs for these animals. In the young specimen of *Chelydra* referred to above the caudal ribs are clearly distinct and are separated from the centra by sutures. In the Ichthyosauria (16) the ribs were free throughout the entire length of the vertebral column. Dr. Williston tells me that he has found free caudal ribs in certain plesiosaurs. In the plesiosaurs, also, Dr. Williston has recently discovered free sacral ribs. From the above enumeration it is clear that caudal ribs are not rare among the reptiles and there can be no doubt, it seems to me, that when a free structure occurs in the sacrum it can be readily homologized with both the presacral and postsacral ribs. In the primitive condition the ribs were not differentiated into dorsals, sacrals and caudals and they varied but little in size. The dorsal and sacral ribs are retained in the majority of reptiles having become functional through use or other cause while the caudal ribs which had no real function to perform have become atrophied or vestigial. Sacral ribs without doubt exist in the dinosaurs. One striking peculiarity of the sauropod dinosaur sacrum is the elongate character of the diapophyses which in many cases serve to aid the sacral ribs in the support of the ilium. This condition obtains in the sacra of *Apatosaurus* and *Brachiosaurus* at least. The presence of these diapophyses led Hatcher, without doubt, to contend that the sacral ribs were parapophyses. But so far as I can see the presence or absence of diapophyses could have no effect whatever on the character of the sacral ribs.

Paleontology helps us not at all in determining the primitive condition of the modern terrestrial lizard sacrum. Of *Paliguana* (17) from the Triassic of South Africa only a fragmentary skull is known and from this form in the Trias to *Iguanavus* (18) in the Laramie Cretaceous, a period representing a lapse of millions of years, our knowledge of the terrestrial lizards is a complete blank. Tertiary lizards are represented for the most part by very fragmentary remains and belong, according to our best authorities, to existing families or to families only recently extinct so that they offer no differences in the morphology of the sacrum from the existing forms.

Nor do the allies of the lizards, the mosasaurs, aigialosaurs and dolichosaurs, offer any clue to the primitive condition of the sacrum. In the Mosasauria, according to Dr. Williston, there is never any sacrum, but the ilia are attached directly to the transverse processes of the vertebra which is either the second or third pygal, at least in one genus (19).

The Dolichosauria differ from the Mosasauria in that the former possess a sacrum of two vertebræ (20) but so far as I have been able to determine there has never been made out in these animals any sacral ribs. In *Adriosaurus* (21) no sacral ribs can be detected because the animal is preserved on its back and no attempt has been made, so far as I am aware, to determine the presence or absence of sacral ribs in this specimen. In *Acteosaurus* (22), however, the sacrum is well exposed but shows no evidences of sacral ribs. In *Dolichosaurus* (23) Owen says: "The extremities of the sacral pleuropophyses come into contact in the *Dolichosaurus* but do not coalesce." From Owen's figure it is difficult to make out just what the condition is in the sacrum of this form. The artist has certainly drawn sacral ribs in the figure but this may have been due to fracture or to a misconception on the part of the artist. Owen makes no statement of any sacral ribs.

In the Aigialosauria from the Cretaceous of Lesina the same conditions hold in the sacrum as we have described for the other forms. Gorjanovic-Kramberger (24) figures a skeleton of *Aigialosaurus* which gives no evidence of any sacral ribs nor does the author mention any ribs as occurring in the specimen. The evidence from *Opetiosaurus* (25) is purely negative since the sacral region of the specimen was in a very poorly preserved condition.

It is an interesting question for speculation just why and how such a condition as we have described should obtain in the lizards. It seems most probable that the Lacertilia constitute a branch which came off in pre-Triassic times from some primitive diapsid stem in which the sacral ribs were functional and that later the ribs from some unknown cause became atrophied.

In conclusion I wish to express my sincere thanks to Dr. Frank R. Lillie, under whose direction this work was done, for his kindly interest in my studies and for his advice. To Mr. W.

L. Tower and Mr. R. E. Scammon I am under obligations for the material which they have very kindly placed at my disposal.

BIBLIOGRAPHY.

1. **Schultze, O.**

- '97 Ueber Herstellung und Conservirung durchsichtiger Embryonen zum Studium der Skelettbildung. Verhandlungen der Anatomischen Gesellschaft, Bd. 13, 1897.

2. **Mall, Franklin P.**

- '06 On Ossification Centers in Human Embryos less than one hundred Days Old. Amer. Jour. of Anat., Vol. V., No. 4, pp. 431-458 with 6 text figures and 7 tables. 1906.

3. **Hill, Eben C.**

- '06 On the Schultze clearing method as used in the anatomical Laboratories of the Johns Hopkins University. Bull. of the Johns Hopkins Hospital, Vol. XVII., No. 181, pp. 111-115, 1906.

4. **Siebenrock, Friedrich.**

- '94 Das Skelet der Lacerta Simonyi Steind. und der Lacertiden Familie überhaupt. Sitz. der Kaiserl. Akad. der Wissenschaften in Wien. Mathem.-Naturw. Classe, Bd. CIII., Abth. I., April, 1894.

5. **Gegenbaur, C.**

- '71 Beiträge zur Kenntniss des Beckens der Vögel. Jenaische Zeitschrift., Bd. VI., 1871.

6. **Hoffman, C. K.**

- '77-'78 Beiträge zur vergleichende Anatomie der Wirbelthiere — IX. Zur Morphologie der Rippen. Nederl. Archiv für Zoölogie, Bd. IV., 1877-1878.

7. **Siebenrock, Friederich.**

- '92 Ueber Wirbel-Assimilation bei den Sauriern. Annalen der K.K. Hofmuseums, Bd. VII., 1892.

8. **Cope, E. D.**

- '92 The Osteology of the Lacertilia. Proc. of the Amer. Philos. Soc., Vol. XXX., p. 207, May 10, 1892.

9. **Huxley, T. H.**

- '92 A Manual of the Anatomy of the vertebrated Animals, p. 192, New York, 1892.

10. **Parker and Haswell.**

- '97 Text-Book of Zoölogy, Vol. II., p. 295, London, 1897.

Parker, J. Jeffery.

- '84 A Course of Instruction in Zoöatomy, p. 134, London, 1884.

Thompson, J. Arthur.

- '99 Outlines of Zoölogy, pp. 570, Edinburgh and London, 1899.

Pouchet, G., et Bauregard, H.

- '89 Traite d'Osteologie Comparee, pp. 355, Paris, 1889.

Zittel, Karl A.

- '87-'90 Handbuch der Paleontologie. Abth. I., Bd. III., Vertebrata, p. 605. München & Leipzig, 1887-1890.

11. Gadow, Hans.

'01 Amphibia and Reptiles, pp. 496, London, 1901.

12. Siebenrock, Friedrich.

'95 Das Skelet der Agamidæ. Sitz. der Kaiserl. Akad. der Wissenschaften in Wien. Mathem. Naturw. Classe, Band CIV., Abth. I., p. 66, Nov., 1895.

13. Gegenbaur, Carl.

'98 Vergleichende Anatomie der Wirbelthiere mit Berücksichtigung der Wirbellosen. Bd. I., p. 251, Leipzig, 1898.

14. Hatcher, J. B.

'03 Osteology of Haplocanthosaurus. Mem. Carnegie Mus., Vol. 2, No. 1, pp. 14-22, 1903.

15. McGregor, J. H.

'06 The Phytosauria, with especial reference to *Myrstriosuchus* and *Rhytidodon*. Mem. of the Am. Mus. of Nat. Hist., Vol. IX., Pt. II., p. 69, 1906.

16. Zittel, Karl A.

'87-'90 Handbuch der Paleontologie. Abth. I., Bd. III., Vertebrata, p. 606, München & Leipzig, 1887-1890.

17. Broom, R.

'03 On the Skull of a true Lizard (*Paliguana Whitei*) from the Triassic Beds of South Africa. Records of the Albany Museum, Vol. I., No. 1, p. 1, 1903.

18. Marsh, O. C.

'92 Notice of new Reptiles from the Laramie Formation. Am. Jour. of Sci., Vol. XLIII., p. 450, May, 1892.

19. Williston, S. W.

'04 The Relations and Habits of the Mosasaurs. Jour. of Geol., Vol. XII., No. 1, p. 51, 1904.

20. Woodward, A. S.

'98 Vertebrate Paleontology, pp. 190, Cambridge, 1898.

21. Seeley, H. G.

'81 On Remains of a Lizard, Q. J. G. S., Vol. 37, pp. 52-56, 1881.

22. von Meyer, H.

'60 Paleontographica. Bd. VII., p. 223, Pl. XXIV., 1860.

23. Owen, R.

'51 Fossil Reptilia of the Cretaceous Formations, p. 28, Pl. X., London, 1851.

24. Kramberger, Gorjanovic-Carl.

'92 Aigialosaurus, eine neue Eidechse aus der Kreideschiefern der Insel Lesina. Societas Historico-Naturalis Groatica, p. 20, 1892.

25. Kornhuber.

'01 Abhandlungen der k. k. Geol. Reichsanstalt, Bd. XVII., Heft 5, pp. 1-24 Pls. I.-III., 1901.